SILVICS of PONDEROSA PINE

Figure 1.--Botanical range of ponderosa pine (including varieties).

Misc. Pub. No. 12 June 1957

SILVICS OF PONDEROSA PINE

By

James D. Curtis & Donald W. Lynch
Foresters

INTERMOUNTAIN FOREST AND RANGE EXPERIMENT STATION
Forest Service
U. S. Department of Agriculture
Ogden, Utah
Reed W. Bailey, Director

Foreword

As intensive forest management gradually becomes more common, silviculture will be the means by which the forest will be systematically but carefully manipulated. Silviculture can be really successful only as the silvics of the species are available, appreciated, and applied in the process of removing mature tree crops and starting new ones.

The silvics of the more important North American tree species, as revealed by many years of observation and research, are being collected and published by the U. S. Forest Service experiment stations. This report is one of seven including ponderosa pine, western white pine, lodgepole pine, western larch, western redcedar, grand fir, and black cottonwood being prepared by the Intermountain Forest and Range Experiment Station. Eventually, a single publication that will include the entire series will be issued by the U. S. Forest Service.

The information in this publication is based on selected references and unpublished data through 1956. The authors will appreciate having any omissions or apparent misinterpretations called to their attention.

CONTENTS

SILVICS OF PONDEROSA PINE[1]

By
James D. Curtis and Donald W. Lynch[2]

Ponderosa pine (*Pinus ponderosa*)(76)[3] is the most widely distributed species of its genus in North America (103) extending from Canoe Creek[4] on the Fraser River in British Columbia in the north, to Durango, Mexico in the south. It is found from Holt County, Nebraska (21) to the Pacific Coast (103) (fig. 1).

The earliest published account of the species is in the journal of the Lewis and Clark expedition of 1804. David Douglas, the Scottish botanist, recorded it in 1826 as occurring on the Spokane River and a year later sent seeds to the London Horticultural Society from which a tree was raised in the Caledonian Horticultural Society's garden. The first scientific description was by Lawson in 1836 (137). For many years it was called western yellow pine but the name was officially changed in 1932 by the nomenclature committee of the U. S. Forest Service (7) and generally accepted thereafter.

HABITAT CONDITIONS

CLIMATIC

Judged by Thornthwaite's climate classification (140) ponderosa pine is found generally in a subhumid humidity province and a microthermal temperature province characterized by summer rainfall deficiency. For the east slope of the Rockies, the Black Hills, Utah, and the Southwest, however, summer rains are the rule although the Southwest regularly experiences low May-June precipitation. At selected, typical locations in six western states and British Columbia average annual precipitation varies from 10.20 to 21.48 inches, and average growing season precipitation (May through August) from 1.75 to 6.15 inches. Corresponding figures for the Black Hills of South Dakota are about 28.00 and 13.00 inches respectively, but at the Fort Valley Experimental Forest near Flagstaff,

---

1/ This statement, in essentially the same form, together with those of other silviculturally important tree species of the United States, will appear shortly as a U. S. Department of Agriculture bulletin.

2/ Foresters, Intermountain Forest and Range Experiment Station, U. S. Forest Service, Ogden, Utah and Boise, Idaho, respectively.

3/ Numbers in parentheses refer to Literature Cited, page 24.

4/ Unpublished data furnished by Research Division, British Columbia Forest Service, Victoria, British Columbia.

Arizona, 6.22 inches of the total growing seasonal precipitation of 7.63 falls in July and August following the May-June dry period. The Skagit valley of northwest Washington and Challenge (U. S. Forest Service Ranger Station) in north-central California where annual rainfall reaches 41.06 inches and 68.80 inches may be two of the wetter areas supporting ponderosa pine in any quantity[4, 5, 6, 7, 8/] (112, 147).

The extent of the seasonal rainfall deficiency is better appreciated when it is realized that commonly July and August (May and June in Arizona) precipitation is about 1 inch or less, but that in some places, and frequently in California, it is lacking. Showers that follow early summer droughts probably provide scant moisture useful to young seedlings. In other words, total growing season precipitation figures are misleading and mean little because of the distribution pattern, an unreliable and unpredictable phenomenon.

Regardless of location where ponderosa pine grows, average annual temperatures are between 41.8° and 49.8° F., and average July-August temperatures between 62.0° and 69.6° F. Annual extremes are from -37° to 107° F. 4, 5, 6, 7, 8/

EDAPHIC

Ponderosa pine grows on soils of igneous, metamorphic, and sedimentary origin including quartzite, argillite, schist, shale, basalt, andesite, granite, cinders, pumice, limestone, and sandstone. This results in a variety of soil types (textural classes) including sandy (granitic) loam, gravelly loam, silt loam, clay loam, loamy sand, sandy (basaltic) loam, and gravel on which the species is found throughout its extensive range[4, 5, 6, 7, 8/] (14, 111, 157). Depending on the locality and the horizon from which samples are taken ponderosa pine soils have been found to vary from pH 4.93 to pH 9.10[6/] (14, 41). Frequently the pH will vary from 6.0 to 7.0 in the surface horizon. Soil samples to a depth of 24 inches in the Boise Basin in central Idaho were found to be

5/ Unpublished data furnished by Rocky Mountain Forest and Range Experiment Station, U. S. Forest Service, Fort Collins, Colorado.

6/ Unpublished data furnished by Missoula Research Center, U. S. Forest Service, Missoula, Montana.

7/ Unpublished data furnished by California Forest and Range Experiment Station, U. S. Forest Service, Berkeley, California.

8/ Unpublished data furnished by Pacific Northwest Forest and Range Experiment Station, U. S. Forest Service, Portland, Oregon.

largely neutral (pH 6.6 to pH 7.3) in reaction.[9/] The species probably reaches its best development on well-drained, deep sandy, gravel, and clay loams. This is borne out by its performance on such sites (88, 99) and its frequent absence where an impervious substratum exists. This may take the form of associated species encroachment, as the occurrence in certain localities of lodgepole pine in groupwise fashion when good drainage is prevented by the presence of clay subsoil (60). It has also been shown that the texture of the soil mantle, and thus its moisture-retaining capacity, plays an important role in the tree's development, possibly more so than the chemical constituents (59, 111, 138).

On selected areas in Utah, Arizona, Colorado, and Idaho, water-holding capacities of the soil varied from 25.8 to 70.0 percent, and wilting coefficients from 3.3 to 16.1 percent[9/] (14).

PHYSIOGRAPHIC

Ponderosa pine extends from latitude 51°35' N. and longitude 122°25' W. in the Fraser River drainage of British Columbia to approximately latitude 24°00' N. and longitude 104°45' W. in west-central Mexico, and from latitude 42°30' N. and longitude 99°30' W. in northeastern Nebraska to the Pacific Coast in California. The southernmost range in Baja California is stated to be in the isolated peaks of the Sierra San Pedro Marino (31) but more recent investigations indicate the southern extremity as Julian and San Luis Rey Canyon in San Diego County (43). This may be considered its botanical range. Within this vast area outlined by 15 states, Mexico, and one Canadian province, commercial stands of this valuable species are found in British Columbia, Washington, Oregon, Idaho, Utah, Montana, South Dakota, Colorado, Nebraska, New Mexico, Arizona, California, and Mexico (136, 137, 146).

Ponderosa pine is found at elevations from sea level near Tacoma, Washington (56) to about 9,000 feet in California, Colorado, and Arizona[5, 7/] (111). From north to south throughout its range the species tends to grow at progressively higher altitudes. Although exceptions can be found, the stands of best development occur at elevations of 4,000 to 8,000 feet (depending on latitudinal location) on benches, plateaus, and west and south aspects where the competition from other tree species is not too severe. Such species might include: Douglas-fir (*Pseudotsuga menziesii*), but also lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), white fir (*Abies concolor*), grand fir (*A. grandis*), sugar pine (*Pinus lambertiana*), and incense-cedar (*Librocedrus decurrens*), depending on the forest type.[4, 5, 6, 7, 8/]

9/ Unpublished information. Intermountain Forest and Range Experiment Station, U. S. Forest Service, Ogden, Utah.

"A"

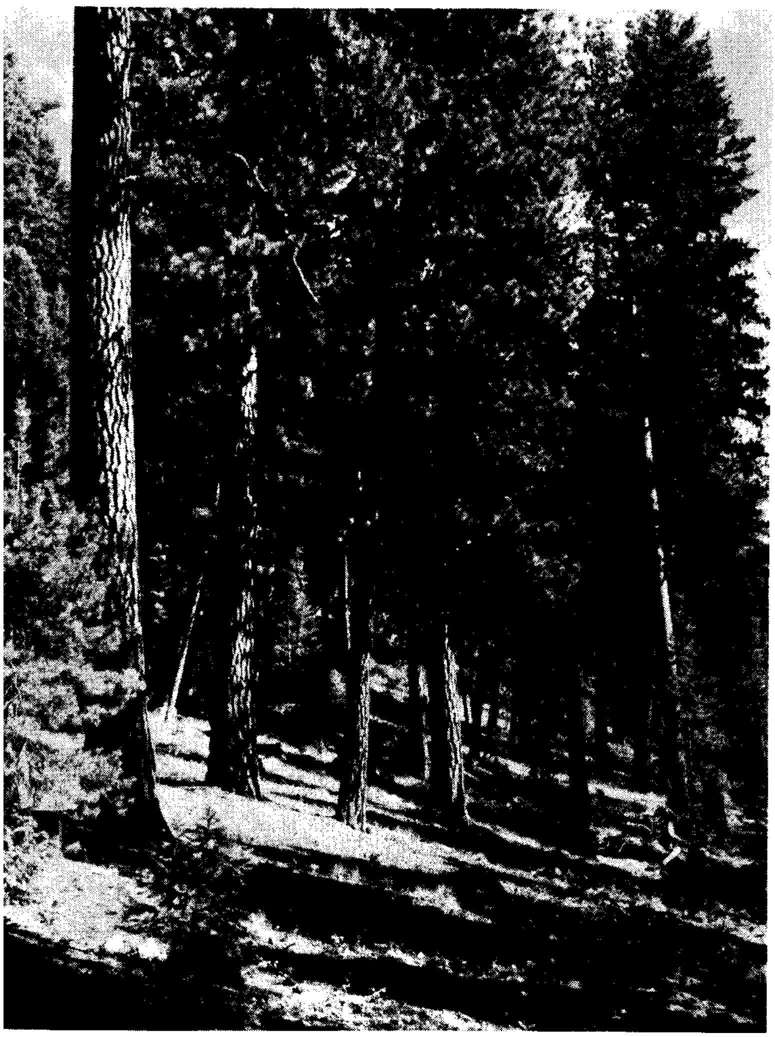

Figure 2.--The ponderosa pine type is commonly composed of many small, even-aged stands, up to an acre or so in size, often pure but sometimes in mixture. In the older age classes, the absence of shrubs and tree seedlings gives the impression of a parklike forest. "A" shows three distinct age classes of trees in a pure stand and "B" a view within one of the older age classes.

"B"

BIOTIC

Ponderosa pine is largely contained within the arid transition zone of the West (85). It may be classed as a component of the Montane Forest, and more specifically the Petran Montane and the Sierran Montane Forests (150). It is further considered the most xeric of the major dominants of this plant association. It is also pointed out that this species forms a consociation and climax unit where it occurs in the pure form or as an association with one or two other tree species, at least over an extensive part of its range (28). Characteristically, ponderosa pine tends to grow in groupwise arrangement of age classes particularly where it occurs in pure stands (fig. 2).

Ponderosa pine can be found as an integral component of five forest cover types in the West including the ponderosa pine--larch--Douglas-fir, interior ponderosa pine, ponderosa pine-sugar pine-fir, Pacific ponderosa pine--Douglas-fir, and Pacific ponderosa pine. The first is typical in western Montana and one in which ponderosa pine never predominates. With cutting or increase in moisture it is easily transformed into either the larch--Douglas-fir type or just the Douglas-fir type (130).

The interior ponderosa pine type comprises the greater part of the area over which the species occurs in eastern Oregon and Washington, Idaho, western Montana, South Dakota, the east slope of the Sierra Nevada in California, Utah, western Colorado, Arizona, and New Mexico. It is frequently found in pure stands and elevationally is the first forest type (sawtimber) of consequence above the desert floor. It is found mingled with Douglas-fir, white fir, western larch, aspen (*Populus tremuloides*), and lodgepole pine towards its upper limits where moister sites prevail by virtue of either aspect or soil conditions. It is commonly a climax type (130).

The ponderosa pine-sugar pine-fir type is often called the "mixed conifer type" in California where it is most extensive on the "west side" of the Sierra Nevada. It is characterized by the predominance of ponderosa pine, sugar pine, white fir, Douglas-fir, or incense-cedar, singly or in combination. The type is found at 3,000 to 6,000 feet elevation and is considered a climax form (130).

The Pacific ponderosa pine--Douglas-fir and the Pacific ponderosa pine types are found in northern California and also in southern Oregon. They are both found with varying numbers of associated species. The former occur typically in the north coast ranges, the Siskiyou Mountains and southern Cascades; the latter on the lowermost west slopes of the Sierra Nevada and southern Cascade range and cross ranges of northern California and southern Oregon. The latter is a climax type; the former is not (130).

Within the ponderosa pine zone of northern Idaho and extreme northeastern Washington, the understory plant cover can be classified usefully by recognizing habitat groups. Thus, four associations (P. P/*Physocarpus*,

P. P./Symphoricarpos, P. P./Agropyron, and P. P./Purshia) are easily discernible in which ponderosa pine predominates and in which it is a major climax species (41).

A variety of vegetation is found in the ponderosa pine type. The following lists are not exhaustive but include the more common woody and herbaceous plant cover found in the different areas where the type occurs:

a. British Columbia: Douglas-fir, Artemisia tridentata, A. tripartita, Arctostaphylos uva-ursi, Purshia tridentata, Symphoricarpos albus, Rosa nutkana, Crataegus douglasii, Clematis ligusticifolia, Agropyron spicatum, Aristida longiseta, and Festuca scabrella.4/

b. Western Montana, Idaho, Oregon, and Washington: Douglas-fir lodgepole pine, aspen, Prunus virginiana, P. pensylvanica, P. virginiana var. melanocarpa, Artemisia tridentata, Chrysothamnus nauseosus, Ceanothus velutinus, Symphoricarpos rivularis, Amelanchier alnifolia, Purshia tridentata, Rosa spaldingi, R. ultramontana, Spiraea betulifolia, Berberis aquifolium, Physocarpus malvaceus, Calamagrostis rubescens, Festuca idahoensis, Stipa columbiana, Koeleria cristata, Bromus tectorum, Balsamorhiza sagittata, and Carex geyeri 6, 8/ (41).

c. California: Douglas-fir, white fir, incense-cedar, sugar pine, Jeffrey pine (Pinus jeffreyi), tanoak (Lithocarpus densiflorus), madrone (Arbutus menziesii), California black oak (Quercus kelloggii), Chamaebatia foliolosa, Arctostaphylos patula, Ceanothus cordulatus, C. prostratus, C. parvifolius, Castanopsis sempervirens, Stipa elmeri, S. occidentalis, Carex rossi, Festuca idahoensis, and Sitanion hystrix.7/

d. Colorado and the Black Hills: Bromus tectorum, Bouteloua gracilis, Festuca arizonica, Agropyron smithi, Muhlenbergia montana, M. torreyi, Danthonia spicata, Geranium fremonti, Sporobolus heterolepis, Koeleria cristata, Poa pratensis, Allium cernuum, Fragaria americana, Galium boreale, Artemisia frigida, Purshia tridentata, Populus tremuloides, Prunus virginiana, Rosa macounii, Opulaster intermedius, Amelanchier alnifolia, Symphoricarpos occidentalis, and Arctostaphylos uva-ursi.5/

e. New Mexico and Arizona: Gambel oak (Quercus gambeli), Achillea lanulosa, Thalictrum fendleri, Lotus wrighti, Vicia americana, Senecio spartioides, Actinea richardsoni, Muhlenbergia montana, Bouteloua gracilis, Festuca arizonica, Blepharoneuron ticholepis, Sitanion hystrix, Agropyron smithi, Sporobolus interruptus, and Koeleria cristata (110).

LIFE HISTORY

SEEDING HABITS

Flowering and fruiting.--Based on available records taken over periods from 3 to 10 years in the five regions where ponderosa pine is found, there appears to be at least as much intraregional as interregional variation for a specific phenological response. In western Montana, central Idaho, and eastern Oregon, at elevations from 3,000 to 6,000 feet above sea level, flowering generally starts May 1 to 10. Female conelets nearly 1 inch long appear May 5 to June 10, pollen is shed May 25 to June 15, cones reach full size July 20 to August 10 of the following year, seed is ripe August 20 to September 5, cones begin to open September 1 to 13, and seed is shed until November.[6, 7, 8/] On the east and on the west side of the Sierra Nevada in California at 6,000 feet altitude, cone development takes place about 2 weeks later (51). In ponderosa pine stands on the west side of the Sierra Nevada in California, cones did not open on the trees until their specific gravities had dropped below 0.62 (127). In northwest Montana, 5.4 percent of total seed production fell from October 30 of one year to May 2 of the next year (133) but occasionally seed is retained an even longer time (105). In Colorado at 8,900 feet studies over a 9-year period disclosed that carpellate flowers emerge on or about June 18 and that only about 36 percent of them survive at the beginning of the second year. Their initial emergence is closely correlated with the passing of freezing weather (120). In the California pine region, trapping indicated that seed fall was complete by the middle of November (51).

In California on the west slopes of the Sierra Nevada, pollen was collected as early as April 15 at 39° N. latitude and 121° W. longitude at 3,000 feet but May 11 was found to be a fair average date over a 7-year period. For this locality it is estimated that a mean interval of 8 days per 1,000 feet difference in elevation can be considered safe for purposes of pollen collection (42).

In common with most other pines, ponderosa pine cones require 2 years to mature, or specifically, about 26 months (120). The species is monoecious having male and female flowers on the same tree (56).

It has been found that fertilization in the cone ovules takes place when the seed is full grown and within a few days, some 13 to 14 months after pollination. Embryonic selection requires 34 to 36 days, embryonic differentiation 10 to 12 days, and seed maturation 40 to 45 days (24). The larger the seed the larger the embryo and the greater the number of cotyledons but there is no correlation between seed size and cone size although a tendency in this direction exists. The number of cotyledons will be found to vary between 6 and 14 (25). Inherent vigor is not correlated with, or transmitted by weight of seed, but weight differences between seeds of ponderosa pine are largely due to the weight of seed coat and endosperm (115).

Seed production.--No periodicity, as such, has been observed in the seed production of ponderosa pine. In California ponderosa pine forests medium seed crops are borne on an average of every 2 years although the average interval between very heavy cone crops is 8 years (51). Observation over 23 years shows the species to be a poor seeder west and a fair seeder east of the Continental Divide in Montana with only one "good" crop occurring (22). The species bears cones at as early as 16 years, which is close to the minimum age for conifers (27) and will continue to produce seed with acceptable viability when 350 years old (37). Seed from trees of 60 to 160 years has been found to possess greater viability than that from younger or older trees (113, 143). In California trees over 25 inches diameter breast high were the best producers (51). In central Idaho, mature and overmature trees at 5,500 feet elevation produced lower quality seed than similar trees at 4,000 feet (143), and open grown trees produced heavier crops of larger cones than stand grown trees (142).

Recent studies indicate a relationship between the total average monthly temperatures for April and May of the year flower buds are formed and the cone crop response 27 months later. Temperatures above normal presage abundant flowering the following spring; temperatures below normal result in few flowers the subsequent year (83).

The insects which do most damage to cones and to seed development are probably *Conophthorus ponderosae* and *Megastigmus albifrons* (63) and may account for considerable loss in years of small cone crops.

Many birds and mammals, including the white-breasted nuthatch (*Sitta carolinensis*), red-breasted nuthatch (*S. canadensis*), longcrested jay (*Cyanicitta stelleri diademata*), Steller's jay (*C. stelleri*), red-shafted flicker (*Colaptes cafer*), junco (*Junco phaeonotus dorsalis*). house finch (*Carpodacus mexicanus*), redpoll (*Acanthis linaria*), red crossbill (*Loxia curvirostra*), Clark's nutcracker (*Nucifraga columbiana*), white-headed woodpecker (*Dryobates albolarvatus*), black-capped chickadee (*Penthestes atricapillus*), Great Basin white-footed mouse (*Peromyscus maniculatus sonoriensis*), Columbian white-footed mouse (*P. maniculatus artemisiae*), thick-footed mouse (sp. ?), pocket mouse (sp. ?), buff-bellied chipmunk (*Eutamias amoenus luteiventris*), western chipmunk (*E. minimus*), pine or red squirrel (*Tamiasciurus hudsonicus*), California gray squirrel (*Sciurus griseus*), Douglas squirrel (*T. douglasii*), silver gray squirrel (*S.* sp.), Abert squirrel (*S. aberti*), Kaibab squirrel (*S. kaibabensis*), Arizona mantled ground squirrel (*Citellus lateralis arizonensis*), and golden-mantled ground squirrel (*C. lateralis*) all consume seed, sometimes in impressive quantities (20, 124), either in the tree or on the ground[8/] (2, 4, 34, 111, 132, 133, 139). In fact, the red or pine, Kaibab, and Abert squirrel destroy prospective cone crops by their vigorous clipping of cone-bearing twigs carrying potential flowers and/or conelets (4, 111, 132). Hence, it is conceded that certain rodents and birds can substantially affect, directly and indirectly, the seed crop in years of low and fair production (34, 111, 132).

In central Idaho ripe cones had a specific gravity of .80 to .86, varied in mean maximum diameter from 1.72 to 1.90 inches and in length from 3.20 to 3.89 inches, and averaged 64 to 92 seeds per cone (142). Generally cones have been found to range from 1.5 to 2 inches in diameter and 2.75 to 5.75 inches in length (51, 137). Cleaned seed per pound varies from 6,900 to 23,000 and averages 12,000. One bushel of cones will produce 9 to 32 ounces of clean seed and 100 pounds of fresh cones will yield 2 to 7 pounds of clean seed. Germinative capacity varies widely but usually averages close to 60 percent (145).

In central Idaho for selected dominants, the mean number of seed per tree for a single year ranged from 16,100 in 70-year-old second-growth at 5,500 feet elevation to 118,300 in virgin overmature stands at the same elevation (142). In California, over a 16-year period, trees over 50 inches d.b.h. averaged 300 cones per tree.[7/] Ponderosa pine seed will retain a high fraction of its original viability if suitably stored (in air-tight containers at 32° F.) (37, 123, 125) but has sprouted during stratification at 36° F. (126). Delayed germination for 1 year has been recorded for the species (37).

Seed dissemination.--The character of stand will largely determine for a given year how many ponderosa pine seeds will reach the ground. In central Idaho 254,000 per acre were recorded for virgin forest, 203,000 per acre in a selectively cut forest (with a residual stand of 4,047 f.b.m. per acre) and 243,000 in a 70-year-old second-growth forest as early as September 15 (144). Seed was produced at the rate of 104,000 per acre in a partially cut stand in western Montana (133). Very little seed is carried more than 100 feet from the edge of timber (144). As a general rule, the heavier the seed, the more rapid the fall but many exceptions to this occur because the size, shape, and curvature of a seed wing varies within a species; indeed, seed size and wing size vary between sizes of cones and the position of the seed in the cone. Ponderosa pine seed with an average weight of .058 gram fell in still air at an average rate of 5.0 feet per second (129). In California, it is estimated that "under average conditions, probably very little seed is scattered more than about 300 feet" (51).

VEGETATIVE REPRODUCTION

Ponderosa pine does not reproduce naturally by vegetative means, although two instances of root inducement (from callus formation after wounding the branch of a young growing tree and surrounding it with damp sphagnum moss enclosed by tightly secured polythene wrapping) are on record.[10/] Propagation of the species by cuttings has been accomplished but is considered still in the experimental stage. The age of the tree from which cuttings are collected and the location of the sample branch in relation to the leader, the time of year, the physiological condition

---

10/ Intermountain Forest and Range Experiment Station unpublished report, 1953.

of shoots, the temperature of the rooting medium and the relation between temperature of the atmosphere and that of the rooting medium, all affect the success of root propagation. Success in rooting, using various media and treatments, has varied between 0 and 68 percent (93).

Ponderosa pine has also been propagated vegetatively by grafting. The methods of grafting seedlings on transplants, seedlings on seedlings, shoots of older pines on nursery transplants, single needle bundles, and by approach (inarching) were all used experimentally. A total of twenty successful intraspecific grafts of the genus *Pinus* was achieved. Ponderosa pine was used as the scion in three cases and as the stock in fifteen (91).

SEEDLING DEVELOPMENT

Establishment.--Throughout its range, excepting the Black Hills, ponderosa pine reproduces spasmodically, which is widely construed as the result of the fortuitous combination of a heavy seed crop followed by an above average rainfall during the growing season. Available evidence (31, 35, 50, 72, 111, 112, 118, 141, 144, 157) indicates that soil moisture is the critical factor of survival. Because of this fact, it follows that soil texture, plant competition, and condition of the seedbed exert decisive influence--separately or collectively--in the survival of the very young seedling. The extent and effect of these influences have been examined, measured, and interpreted[8/] (11, 39, 54, 61, 102, 111, 141, 144, 150). There is some evidence that seedlings benefit from the proximity of moisture-holding and nitrogen-fixing plants (31, 101), but these instances, unfortunately, are the exception rather than the rule.

Because there is less competition and more soil moisture on burned areas compared to virgin forest, the roots of 1-year-old seedlings penetrate deeper and have more laterals on the former than on the latter (141).

In these early stages of the seedling's life certain factors become critical, militating against its normal development, and commonly cause mortality. The cutworm (*Euxoa excellans infelix*) can cause appreciable (in one instance 28.6 percent) damage to seedlings (47). During open winters 1- and 2-year-old seedlings can suffer damage and mortality from frost (55, 157). Certain rodents and birds destroy young seedlings[8/] (139).

It has also been shown that 1- to 3-month-old seedlings are killed by stem temperatures of about 130° F. and greater (12, 142). To produce this lethal stem temperature, at least under laboratory conditions, required an average, surface (sand) temperature some 21° higher, or about 150° F. (12). Ponderosa pine is more successful in resisting high soil surface temperature with increasing age than its competitors so that when 110 days old seedling stems can successfully withstand instantaneous temperatures of 136° to 180° F. (119). Evidence also indicates that

at elevations of 2,760 feet above sea level and on level ground, soil surface temperatures reach 162° F. in July and as high as 136° F. as late as October 15, in the ponderosa pine type in California (82). The striking and substantial effect of shade on soil surface temperatures has also been demonstrated (12, 82).

Where there is high humidity, heat injury to young seedlings increases with increased temperature. Under ordinary atmospheric conditions it is believed that resistance increases due to the cooling effect within plant tissues produced by transpiration (18). In the light of more recent research on the subject, this resistance can also be accounted for by the physical processes of conduction, radiation, or convection (86).

Ponderosa pine is a more extravagant user of readily available moisture than Douglas-fir, Engelmann spruce, or lodgepole pine, but the nourishment in the large seed and its innate ability to send down a fast-growing taproot (fig. 3) enables it to survive on and dominate the more exposed sites or other sites where competition is not high (15). It also possesses the ability as a seedling to withstand prolonged drought (high soil moisture stress) with soil moisture content very close to, or even below, the permanent wilting point (49, 109). Furthermore, under laboratory conditions, it has been determined that dew at night can possibly contribute to survival of ponderosa pine seedlings growing on typical sites where the wilting point of the soil has been reached, usually late in the growing season (135). Thus, by virtue of these characteristics, its lower altitudinal limits are extended beyond those of other associated species (40).

Some observers feel that, because of organized fire protection, a natural thinning process has largely disappeared. It is pointed out that, as a result, dense, even-aged, stagnating stands of the species have developed. Furthermore, the invasion of associated species such as white fir, Douglas-fir, and incense-cedar have crowded out the advance reproduction and weakened the overstory of ponderosa pine thus making it a prey for insects (149). Antithetically, it is believed by others that in the past fire has been instrumental in prompting the typical groupwise occurrence of small even-aged stands in this species (111, 151).

In view of these observations, it is thought that a method of reproduction that creates openings with thoroughly scarified soil and large enough to provide overhead and some side light, yet in some measure furnishes shade from marginal trees would result under average conditions, in at least some regeneration. It is conceivable that some form of shelterwood would also succeed but only where July-August precipitation can provide sufficient soil moisture (perhaps about 3.00 inches) to offset that used by the overstory and the vegetation which may invade

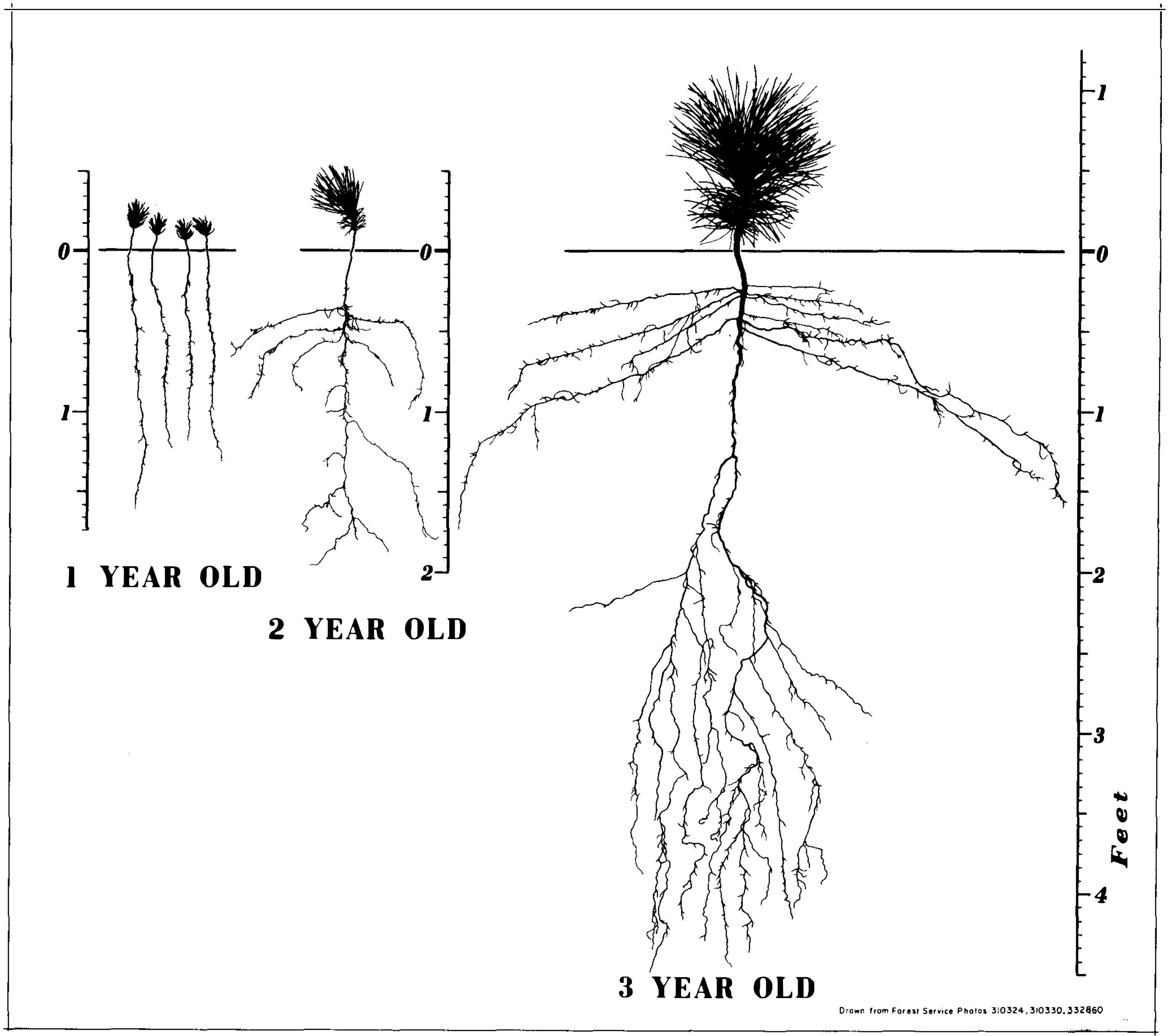

Figure 3.--The development of the seedling root system from initial taproot to one with high and low spreading laterals is illustrated here. First-year seedling taproots as long as 51 inches have been recorded where the growing tip met no obstructing soil layers.

the stand. Considering the systems that have been tried,[11/] however, and the success attending them, it is probable that on areas to be reproduced, even though a seed source and mineral soil seedbed are available, some artificial regeneration will be necessary for acceptable stocking in due time in ponderosa pine management.

Early growth.--The ability of ponderosa pine seedlings to send down a vigorously growing taproot has been given as a reason for its tenacity on severe site where its associates often fail (15). Roots of 1-year-old natural seedlings are known to reach average lengths of 22.4 inches (average top height of 2.8 inches) and 4-year-old seedlings an average maximum of 60.7 inches (average top height of 12.3 inches) on southerly aspects on cutover areas (142). Nevertheless, seedling mortality can be exceedingly heavy (89 percent) during the first year in selectively cut stands (143).

In central Idaho losses attributed to fungi were greater in shade and on north slopes while mortality from insolation was greater in the open and on south slopes. At depths below 6 inches, soil moisture remained above the wilting point on areas free of competing vegetation throughout the growing season but dropped to or below that critical point on most vegetated plots (144). The importance of competing vegetation as a deterrent to early survival and development of young seedlings has been clearly demonstrated in the Southwest (111).

On undisturbed soil, seedlings grow slowly during the first few years of establishment and require full light for best development. Normal growth is hindered by less than 40 percent of full sunlight, but later the form and quality of seedlings are profoundly affected by the amount of side shade they receive (111). Other workers have determined that minimum light requirements vary between 1.60 and 17.0 percent (the former an intensity rarely encountered in pine forests), but point out that soil moisture, and indirectly plant competition and soil texture, play an inseparably allied part in the minimum amount of light the species can endure (16, 26).

Although ponderosa pine seedlings can withstand overstory shade and root competition for as long as 40 years, it is considered an intolerant species (13). The idea has also been advanced that ponderosa pine stands may occur in groupwise fashion by virtue of the tree's intolerance (68).

In central Idaho root growth of 1-year-old seedlings was found to continue throughout the summer in both burned areas and virgin stands, but top growth stopped by August 1 (141). In the seedling stage, ponderosa pine because of its deep root system, even under conditions

11/ Curtis, James D., and Wilson, Alvin K. A test of group selection in Idaho ponderosa pine. Intermountain Forest and Range Experiment Station. (In preparation.)

exposed to wind, is able to maintain a more uniform transpiration rate than, for example, lodgepole pine. It is, therefore, not likely to experience soil moisture fluctuations at the depth to which it penetrates (52) and thus has a distinct advantage over some of its shallower-rooted associates.

On the western slopes of the Sierra Nevada, variation has been found among tree species in the start of seasonal growth. Height growth of ponderosa pine started very significantly later with each rise of 2,000 feet in elevation, and the length of the growing season was shorter significantly with a 3,000-foot increase in elevation. Likewise, radial growth started significantly later with a 2,000-foot increase in elevation. Rates of height and radial growth did not vary with elevation during the grand period of growth. At 5,000 feet elevation a 6-year-average showed that ponderosa pine started radial growth on March 23 and height growth on April 26. The former period lasted 177 days; the latter, 97 days (48).

The depredations that plague the formation, ripening, and safety of seed continue after seedling establishment and during early growth. The meadow mouse (*Microtus* sp.), deer mouse (*Peromyscus* sp.), gray-collared chipmunk (*Eutamias cinereicollis cinereicollis*), Oregon ground squirrel (*Citellus richardsonii*), golden-mantled ground squirrel (*C. lateralis*), pocket gopher (*Thomomys talpoides*), wood rat (*Neotoma cinerea*), rabbits (*Lepus* and *Sylvilagus* sp.), porcupine (*Erethizon epixanthum*), antelope (*Antilocarpa americana americana*), white-tailed deer (*Odocoileus virginianus macrourus*), and mule deer (*O. hemionus hemionus*) feed to a greater or lesser extent on seedlings (1, 3, 17, 32, 111, 114, 139, 156).

Discouragingly enough, but fortunately in isolated instances only, deer can virtually eliminate advance reproduction from the stand (104). Only judicious regulation of grazing can effectively reduce excessive damage to natural and artificial reproduction from sheep and cattle by browsing, trampling, and bedding (111, 131).

Although trees in the sapling and pole stage are less likely to be fatally affected than seedlings, they nevertheless do not escape destructive agencies. Red, Abert, and Kaibab squirrels and porcupines attack saplings and poles and while rarely killing them, produce disfigurement in the stems on which they feed (38, 111, 114).

Uncontrolled fire in central Idaho was found to destroy 87.5, 85.6, and 61.2 percent of the reproduction in virgin, cutover, and young growth stands respectively (30). Even controlled burning has been found exceedingly lethal to the youngest age classes.[12]

12/ Gaines, Edward M., Kallander, Harry R., and Wagner, Joe A. Controlled burning in southwest ponderosa pine: results from the Blue Mountain plots, Fort Apache Indian Reservation. (To be submitted to Jour. Forestry for publication.)

Ordinarily each season, ponderosa pine, by normal physiological processes, develops hardiness to severe winter temperatures (107), but occasionally can suffer "winter killing" of foliage if sudden temperature inversions occur. Likewise, lethal gases can damage the foliage of immature and mature trees (79, 128).

Snow can result in damage to saplings and poles particularly where high stand density has resulted in supple stems and low crown-tree height ratios (111, 142). The engraver beetle (*Ips* spp.) kills sapling and pole-sized trees and can cause extensive damage in young stands (63).

SAPLING STAGE TO MATURITY

Growth and yield.--Ponderosa pine grows to impressive size, and while stems 103.5 inches in d.b.h. (9) and 232 feet in height (56) have been recorded, diameters of 30 to 50 inches and heights of 90 to 130 feet are common throughout most of its range. It often reaches ages of 300 to 500 years in overmature stems, but 726 years have been accurately determined in eastern Oregon (64).

As an example of the yields of ponderosa pine, table 1 shows a representative section from a normal yield table (87), for sites 70 to 100. The full range of site indices for ponderosa pine extends from 40 to 160; site index here refers to height in feet for dominant stand at age 100. Typical stands are irregularly stocked; thus the use of normal yield tables over any sizable area is difficult. The yields in

Table 1.--Board-foot volume[1/] per acre, Scribner rule of trees 11.6 inches and larger in diameter

Age (years)	Volume per acre by site index 2/			
	70	80	90	100
110	16,200	23,100	31,100	40,600
120	19,000	26,200	34,700	44,600
130	21,500	29,000	38,000	48,300
140	23,700	31,500	40,900	51,700
150	25,700	33,800	43,600	54,800
160	27,500	35,900	46,100	57,600
170	29,200	37,800	48,400	60,100
180	30,900	39,600	50,500	62,400

1/ In 16-foot logs to 8-inch top, exclusive of 2-foot stump, measured to nearest 100 board feet.
2/ Site index defined as height in feet for dominant stand at age 100 years.

table 1 should therefore be reduced, because of the common understocking that exists in natural stands, by percentages of 50 or more even for the "well-stocked" condition (33). Typical stands contain fewer stems with larger average diameters than those shown in normal yield tables. However, exceptions to this can be found in restricted areas on poorer sites where overstocking often results in a stagnation of growth. In the Southwest, more extensive areas of overstocked stands exist, particularly in the sapling and pole sizes.

On excellent sites, ponderosa pine is capable of growing at exceptionally fast rates. Growth of young stands on small plots in bottom land areas of northern Idaho was found to average more than 1,000 board feet per acre per year over a 17-year period (80). More typical of average growth of young trees, however, are the rates shown (81) for stands in the Inland Empire. Table 2 gives a portion of a growth table from this study for a 10-year period by diameter and age classes.

Table 2.--Future 10-year volume growth per tree in cubic feet for average sites[1/]

	Age in years			
	40	50	60	70
Inches	Cubic feet			
8	3.50	2.38	1.80	1.46
9	5.40	3.77	3.00	2.50
10	7.45	5.25	4.20	3.63
11	10.40	6.70	5.30	4.50
12	-	8.90	6.95	5.90
13	-	11.20	8.80	7.50
14	-	-	10.30	8.80
15	-	-	12.60	10.70

1/ Includes stump and top without bark.

Heights attained at various ages are shown in figure 4 for several site indices (88). These cover the average range of conditions throughout the ponderosa pine type.

Old-growth ponderosa pine produces excellent, high grade lumber, but young trees are typically limby and natural pruning develops slowly (fig. 5). An average clear length of 11.5 feet has been recorded in stands 250 years old in central Idaho (142). While natural pruning is mostly due to the effect of shade and mechanical forces of nature, an instance is cited in Arizona where the process of branch dying and disintegration was largely due to disease (78).

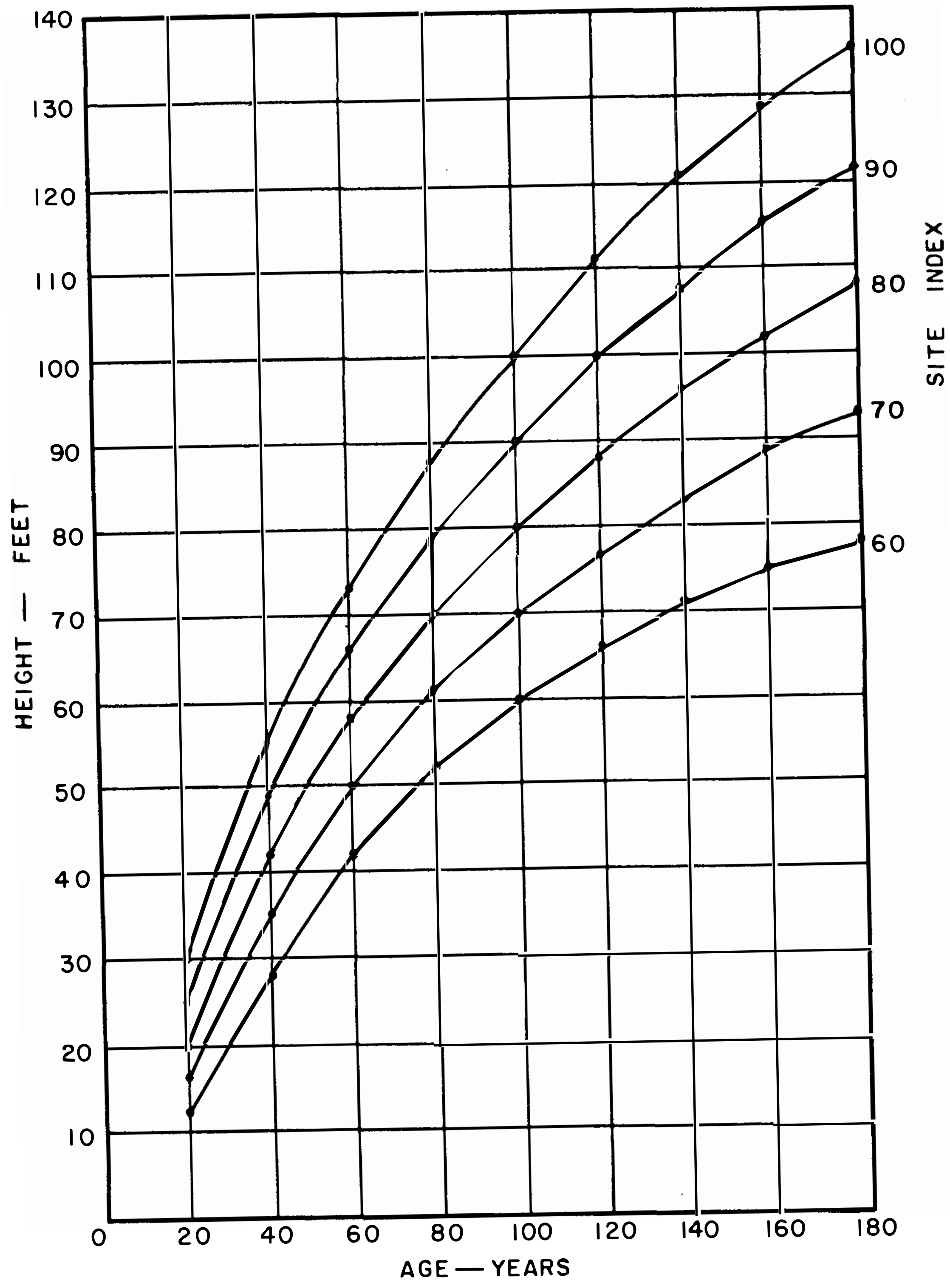

Figure 4.--Heights of the dominant stand of ponderosa pine by ages for site indices 60 to 100 (after Meyer).

Figure 5.--Ponderosa pine is slow to lose its branches as demonstrated in this 80-year-old stand. Artificial pruning will be necessary to produce clear lumber during the 160-year rotation contemplated for the species.

Release.--Ponderosa pine has the ability to respond to release, regardless of age, by increased diameter and/or height growth (36, 45, 69, 70, 87, 98, 111). It is generally accepted that this trait of the species, at least in the older stems, exerts itself largely as a result of increased moisture supply rather than crown expansion, because otherwise the response would not be so sudden although it could be as great. It is noteworthy that this response is manifested even in the oldest (class 4) and the least vigorous (class D) of Keen's tree classes (36, 65).

INJURIOUS AGENCIES

Insects.--From the sapling stage to maturity, ponderosa pine is subject to attack by many kinds of insects. They may attack any part of the tree, from the seeds in the cones to the main trunk. They may reduce the vigor and make the tree more susceptible to attack by other insects, reduce the rate of growth, deform the stem, or kill the tree outright. There are 108 species listed that attack the previously recognized Pacific Coast form and 59 species that attack the previously recognized Rocky Mountain form (63). The appearance, age, and condition of trees has been used as a basis for their susceptibility to insect attack (65, 121).

The most important of the tree-killing insects are several species of *Dendroctonus*. The western pine beetle (*D. brevicomis*) is a common cause of mortality in overmature, decadent, or unvigorous trees. When optimum conditions prevail, it can kill apparently healthy trees of all age classes (155). The Black Hills beetle (*D. ponderosae*) is the most aggressive and destructive enemy in the central Rocky Mountain Region. During the 1895-1908 outbreak in the Black Hills of South Dakota, this insect killed between 1 and 2 billion board feet of ponderosa pine (19). The mountain pine beetle (*D. monticolae*) is an equally aggressive insect but perhaps not quite as frequent in attack (46). *D. barberi*, *D. convexifrons*, and *D. valens* are additional important species of the genus.

Many additional species of bark beetles and flatheaded and roundheaded borers attack ponderosa pine. Most of them enter trees killed or weakened by other agents; but thrifty, vigorous trees are not always immune to attack by some species.

Several defoliating insects such as the pine butterfly (*Neophasia menapia*), the pandora moth (*Coloradia pandora*), and sawflies (*Neodiprion* spp.) periodically cause damage over extensive areas, an example of which was the recent outbreak of the pine butterfly in central Idaho (106).

Tip moths (*Rhyacionia* spp.) often cause terminal and branch killing on saplings, and thus deform the stems. Many kinds of scales, aphids, and other sap-feeding insects can reduce the vigor of the host and thus make it susceptible to additional attack.

Because great volumes of overmature trees are not yet harvested, the *Dendroctonus* beetles are currently considered the most damaging insect, but as this age class of tree is gradually removed, it is possible that other insects may become more important.

Diseases.--A number of pathogens attack ponderosa pine and either kill the host or result in serious defect. One of the more insidious, whose identity is difficult to detect by virtue of its life cycle, is a root and butt rot, *Fomes annosus*. It attacks all ages of trees and, in the case of stems other than small ones that die, is

often mistaken for the work of Dendroctonus beetles which invariably follow the killing of the cambium near the ground level (148).

Polyporus anceps is the major defect from disease in merchantable stands of ponderosa pine in Arizona, New Mexico, and the Black Hills of South Dakota. It gains access to its host through dead branches and may result in a 15-foot column of rot at 150 years of age which involves considerable cull (6).

A serious parasitic destroyer and deformer of the species is dwarf-mistletoe, of which there are two species, Arceuthobium vaginatum forma cryptopodum in the Southwest, and A. campylopodum forma campylopodum in California and the Northwest. It is one of the three major causes of timber mortality in Arizona reaching as much as 16,000,000 board feet annually. Seed can infect trees up to 70 feet distant (53, 67).

Elytroderma deformans, first observed in parts of Idaho, Washington, and Montana in 1913 and described shortly thereafter (154), is found over the entire commercial range of ponderosa pine. It is a serious needle blight capable of slowing growth and killing trees of sawtimber size. Bark beetles are prompted to attack infected trees (75). Severe damage has been reported from the Ochoco National Forest in Oregon where from 1946 to 1950, some 90 percent mortality occurred in areas of severest infection and where 98,148,000 board feet of dying and dead trees were removed (74).

Additional pathogens to which ponderosa pine is subject are the blister rusts. The paintbrush blister rust (Cronartium filamentosum) common in the Southwest (111) and in southern Utah (89) may attack the base, middle, or top of the tree crowns, and spread upward and/or downward rather slowly, eventually killing many merchantable stems. The western gall rust (C. coleosporioides) can be destructive to seedlings and saplings by deforming or killing them (23). It has been found to kill occasional trees and deform larger stems in a 50- to 175-year stand in an isolated area of western Montana (73). C. comandrae (C. pyriforme) produced understocking in seedling, sapling, and pole-sized trees in northeastern California (84).

Fire.--It is common to find basal fire scars on the thick-barked stems in old-growth ponderosa pine forests (fig. 6), and judging from the callus growth on some of these wounds, light uncontrolled fire must have been common before the advent of the white man. In a 45,000-acre conflagration in central Idaho, fire destroyed, and fatally damaged, 73.0, 74.0, and 54.0 percent of the volume in virgin, cutover, and young growth stands respectively (30). Studies on the Modoc National Forest in California revealed extensive but less damage by fire scarring to ponderosa pine than to incense-cedar and also fewer enlargements of old fire lesions (71). In a 1,500-acre burn in Arizona on an area which had been cut by the group selection method and which was a combination of surface and crown fire, no poles and only 5 percent of sawtimber-size trees were living 6 years after the fire where more than 60 percent of the crown

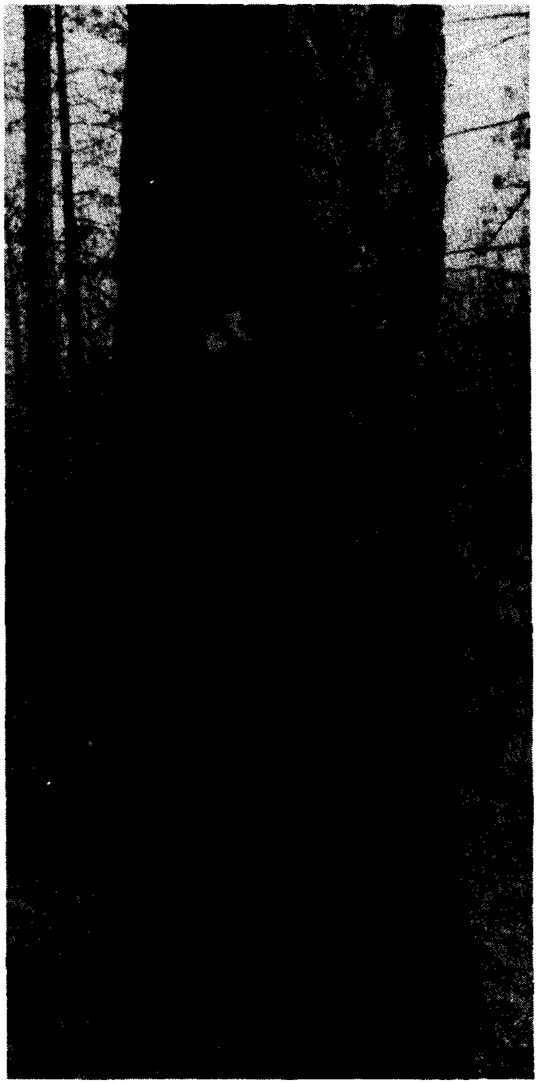

Figure 6.--In old-growth ponderosa pine forests, few mature and overmature trees are without basal fire scars. They are usually not as high as the one shown here but invariably exhibit the effects of more than one surface fire by the presence of successive layers of callus growth on their perimeters.

had been destroyed. From this study it is considered that trees of any size with more than 60 percent of their crown destroyed are poor risks (58).

Considering relative fire resistance of the various species at a mature age, it has been estimated that for the 11 most silviculturally important conifers of the Northern Region, ponderosa pine ranks second, and is indicated as "very resistant," exceeded only by western larch. For 13 important conifers of Oregon and Washington, it is rated third behind western larch and Douglas-fir (134).

Wind.--Because the initial taproot of ponderosa pine generally persists throughout its life, together with strong laterals extending eventually from the base of the tree as far as 100, and occasionally 150 feet (157), it is usually considered a windfirm species. When windthrow does occur it is often because root rots have weakened the tree's stability. In order of decreasing resistance, the species has been listed second out of 10 of the most important Northern Region coniferous species and is exceeded only by western larch.13/ Wind and lightning are nevertheless the two most serious sources of damage to trees of sawtimber size (especially over 30 inches d.b.h.) in the Southwest (111) where, on limestone sites, the root systems are apparently shallow.

13/ Marshall, Robert. Natural reproduction in the western white pine type. Ms. Inland Empire Research Center, U. S. Forest Service, Spokane, Wash. 1928.

SPECIAL FEATURES

Ponderosa pine derives its name from the ponderous bulk of the tree and the weight of the wood sawn from it (76). Phylogenetically it is considered a younger form than Jeffrey pine if its distribution and iodine content are used as criteria (90). Western Indians are reported to have found the living cambium layer sweet and nutritious (8).

The leaves of ponderosa pine are bluish-green or grayish-green and occur in bundles of three (occasionally of two or four and exceptionally of five). Each season's growth of leaves remains on the tree about 3 years (29, 137). It has been found that certain anatomical and morphological features of the needles differ strikingly depending on the age of the tree, the exposure, and the amount of light available (57). Carbohydrate concentrations in needles show distinguishable variations and high correlations with age of foliage and with season, which serve to explain their resistance to damage in cold weather (29).

Hormone concentration has been found to be consistently higher in fast-growing than in slow-growing young ponderosa pine. In the slow-growing trees the leader always contained more auxin than the side shoots. It was concluded from these studies that higher concentration of the growth hormone (which parallels vigor) is a hereditary trait (92).

Ponderosa pine has the ability to develop abnormal leaves arising from the hypertrophy of the scales after certain types of injury. The characteristics of these atavistic leaves are interpreted as suggesting the possibility of remote ancestry (77). The recovery process subsequent to browsing injury on 7-year-old seedlings of the species has been described as "substitute budding" and "substitute growth" (32).

The average content of acetone-soluble extractives in ponderosa pine varies considerably between sapwood and heartwood, being within the limits of 2.0 to 9.8 percent for the former and 3.5 to 31.5 percent for the latter, of the dry weight of wood (5). Resin can constitute as much as 86.4 percent of the oven-dry weight of the wood after extraction, and the lower the stocking of the stand, the larger the tree crown, and the lower in the tree the sample is taken, the higher is the resin content of the wood (108).

The gum turpentine of ponderosa pine characteristically contains, with very few exceptions, large quantities of d-delta-3-carene mixed with pinenes (95). The former constituent was undiscovered when the earliest investigations on the subject were made (122). The ratio between the pinenes and the carene in different trees of ponderosa pine may vary, as shown by fluctuation of the optical properties in individual samples. In certain localities within its range, some trees of the species may provide dextro-rototary terpenes; others may provide levo-rototary terpenes. Furthermore, the different forms, races, and hybrids of the species can each have their own peculiar turpentines (94). In fact, this point can be used

to determine the relationship of closely allied species (96). Gum turpentine from a ponderosa pine in northern Idaho contained about 1 to 2 percent dl-Alpha-pinene; 12 percent l-Beta-pinene; 5 percent Beta-myrcene; 64 percent d-delta^3-carene; 5 percent l-limonene; 2 percent menthyl chavicol, and 4 to 5 percent sesquiterpenes, part of which is cadinenelike sesquiterpene (62). Samples throughout its United States and Canadian range indicate that the yield of turpentine will vary from 15 to 26 percent (94).

RACES AND HYBRIDS

Although ponderosa pine includes a number of geographic races over its widespread range only one variety (*Pinus ponderosa* var. *arizonica*) is recognized (76). The so-called Rocky Mountain form (as contrasted to the Pacific Coast form and designated as *Pinus ponderosa scopulorum*) occurring east of the Continental Divide, in the Central Plateau of western Colorado, Utah, eastern Nevada, Arizona, and New Mexico is believed by some to be a true variety due to anatomical or morphological differences (66, 111). Other investigators consider these differences purely a result of environment and adaptation (76, 137).

It has been shown that, at least in the first 25 years of a tree's life, races of ponderosa pine grown from seed collected from five geographical zones delimited by annual precipitation, exhibit a recognizable number of characteristics such as number of needles in the fascicle, needle length, internal needle structure, and tree growth rate which are considered as being inheritable (152). A somewhat similar investigation, with the added feature of three altitudes of planting (963 feet, 2,730 feet, and 5,650 feet above sea level), instead of one, revealed, in general, the same results. After 12 years of growth, plants from seed collected at 1,500 to 3,500 feet above sea level grew most in each of three planting sites (97). Still other experiments with transplants from seed collected over a considerable part of the species range have emphasized the great variation in average height (8.9 to 14.5 feet) that can be expected 18 years after planting. If average heights of trees on the five different planting sites are considered, the variations in heights are even more pronounced (2.2 to 20.8 feet) (10, 100). Thus the wisdom of using correct seed sources should be obvious to those who expect desirable development of the species when trees grown from seed of a specific climate and physiographic zone are employed in regeneration in a different locality.

A number of successful hybrids have been produced by crossing ponderosa pine with other races and species including *Pinus montezumae*, *P. ponderosa scopulorum*, *P. ponderosa arizonica*, *P. washoensis*, *P. latifolia*, and *P. jeffreyi* (44, 116, 117, 153).

LITERATURE CITED

1. Adams, Lowell
   1949. The effects of deer on conifer reproduction in northwestern Montana. Jour. Forestry 47: 909-913.

2. ______
   1950. Consumption of ponderosa pine seed by small mammals. North. Rocky Mountain Forest & Range Expt. Sta. Res. Note 80, 4 pp. /Processed./

3. ______
   1951. White-tailed deer browsing on natural conifer seedlings. North. Rocky Mountain Forest & Range Expt. Sta. Res. Note 105, 3 pp. /Processed./

4. ______
   1955. Pine squirrels reduce future crops of ponderosa pine cones. Jour. Forestry 53: 35.

5. Anderson, A. B.
   1945. Chemistry of western pines: distribution and nature of acetone soluble extractives in ponderosa pine. Indus. and Engin. Chem. Indus. Ed. 38: 450-454.

6. Andrews, Stewart R.
   1955. Red rot of ponderosa pine. U. S. Dept. Agr., Agr. Monog. 23, 34 pp., illus.

7. Anonymous
   1932. Ponderosa pine now official. Jour. Forestry 30: 510.

8. ______
   1933. Ponderosa pine. Amer. Forests 39: 268-269.

9. ______
   1956. These are the champs. Part II. Amer. Forests 62: 33-40.

10. Austin, Lloyd
   1932. Hereditary variations in western yellow pine. Abstract of address before Calif. Bot. Soc. Madroño 2(7): 62-63.

11. Baker, F. S.
   1925. Character of the soil in relation to the reproduction of western yellow pine. Jour. Forestry 23: 630-634.

12. ______
   1929. Effect of excessively high temperatures on coniferous reproduction. Jour. Forestry 27: 949-975.

13. Baker, F. S.
1949. A revised tolerance table. Jour. Forestry 47: 179-181.

14. ______, and Clarence F. Korstian
1931. Suitability of brush lands in the Intermountain region for the growth of natural or planted western yellow pine forests. U. S. Dept. Agr. Tech. Bul. 256, 83 pp., illus.

15. Bates, Carlos G.
1924. Physiological requirements for Rocky Mountain trees. Jour. Agr. Res. 24: 97-164.

16. ______, C. G.
1925. The relative light requirements of some coniferous seedlings. Jour. Forestry 23: 869-879, illus.

17. ______
1927. Varietal differences. Jour. Forestry 25: 610.

18. ______, and J. Roeser, Jr.
1924. Relative resistance of tree seedlings to excessive heat. U. S. Dept. Agr. Bul. 1263, 16 pp.

19. Beal, J. A.
1939. The Black Hills beetle. U. S. Dept. Agr. Farmers' Bul. 1824, 21 pp., illus.

20. Berry, S.
1914. Work of California gray squirrel on conifer seed in the southern Sierras. Soc. Amer. Foresters Proc. 9: 95-97.

21. Bessey, C. E.
1895. Notes on the distribution of the yellow pine in Nebraska. Gard. and Forests 368: 102-103.

22. Boe, Kenneth N.
1954. Periodicity of cone crops for five Montana conifers. Mont. Acad. Sci. Proc. 14: 5-9.

23. Boyce, John Shaw
1938. Forest pathology. First edition. McGraw-Hill Book Co. Inc., New York. 600 pp., illus.

24. Buchholz, John T.
1946. Volumetric studies of seeds, endosperms, and embryos in Pinus ponderosa during embryonic differentiation. Bot. Gaz. 108: 232-244.

25. Buchholz, John T., and M. L. Stiemert
1946. Development of seeds and embryos in Pinus ponderosa, with special reference to seed size. Illinois State Acad. Sci. Trans. 38: 27-50.

26. Burns, George P.
1923. Studies in tolerance of New England trees. IV. Minimum light requirements referred to a definite standard. Vermont Agr. Expt. Sta., Burlington, Vermont. Bul. 235, 32 pp.

27. Büsgen, M., and E. Münch
1931. The structure and life of forest trees. (English transl. by Thomas Thompson) Ed. 3, 436 pp., illus. John Wiley & Sons, Inc.

28. Clements, Frederic E., and Victor E. Shelford
1939. Bio-Ecology. John Wiley & Sons, Inc., New York; Chapman & Hall Ltd., London. 425 pp.

29. Clements, Harry F.
1938. Mechanisms of freezing resistance in needles of Pinus ponderosa and Pseudotsuga mucronata. Wash. State College Res. Studies VI(1): 45 pp.

30. Connaughton, Chas. A.
1934. Fire damage in the ponderosa pine type in Idaho. Jour. Forestry 34: 46-51.

31. Cooper, A. W.
1906. Sugar pine and western yellow pine in California. U. S. Dept. Agr. Forest Serv. Bul. 69, 42 pp., illus.

32. Cooperrider, C. K.
1938. Recovery process of ponderosa pine reproduction following injury to young annual growth. Plant Physiol. 13: 5-27, illus.

33. Cummings, L. J.
1947. The relationship of normal to average ponderosa pine stands of north Idaho. Jour. Forestry 39: 47-48.

34. Curtis, James D.
1948. Animals that eat ponderosa pine seed. Jour. Wildlife Mangt. 12: 327-328.

35. ______
1950. Stocking of logged ponderosa pine land in central Idaho. Intermountain Forest & Range Expt. Sta. Res. Paper 23, 15 pp., illus. /Processed./

36. Curtis, James D.
1952. Response to release of ponderosa pine in central Idaho. Jour. Forestry 50: 608-610.

37. _______
1955. Effects of origin and storage method on the germinative capacity of ponderosa pine seed. Intermountain Forest & Range Expt. Sta. Res. Note 26, 5 pp. /Processed./

38. _______, and Alvin K. Wilson
1953. Porcupine feeding on ponderosa pine in central Idaho. Jour. Forestry 51: 339-341.

39. Dahms, Walter G.
1950. The effect of manzanita and snowbrush competition on ponderosa pine reproduction. Pacific Northwest Forest & Range Expt. Sta. Res. Note 65, 3 pp. /Processed./

40. Daubenmire, R. F.
1943. Soil temperature versus drought as a factor determining lower altitudinal limits of trees in the Rocky Mountains. Bot. Gaz. 105: 1-13.

41. _______, R.
1952. Forest vegetation of northern Idaho and adjacent Washington and its bearing on concepts of vegetation classification. Ecol. Monog. 22: 301-330.

42. Duffield, J. W.
1953. Pine pollen collection dates--annual and geographic variation. Calif. Forest & Range Expt. Sta. Res. Note 85, 9 pp. /Processed./

43. _______, and W. C. Cumming
1949. Does Pinus ponderosa occur in Baja California? Madroño 10: 22-24.

44. _______, and F. I. Righter
1953. Annotated list of pine hybrids made at the Institute of Forest Genetics. Calif. Forest & Range Expt. Sta. Res. Note 86, 9 pp. /Processed./

45. Dunning, Duncan
1922. Relation of crown size and character to rate of growth and response to cutting in western yellow pine. Jour. Forestry 20: 379-389.

46. Evenden, James C.
1943. The mountain pine beetle. U. S. Dept. Agr. Cir. 664, 25 pp., illus.

47. Fowells, H. A.
1940. Cutworm damage to seedlings in California pine stands. Jour. Forestry 38: 590-591.

48. ______
1941. The period of seasonal growth on ponderosa pine and associated species. Jour. Forestry 39: 601-608. illus.

49. ______, and G. H. Schubert
1945. Availability of soil moisture to ponderosa pine. Jour. Forestry 43: 601-604.

50. ______, and ______
1951. Natural reproduction in certain cutover pine-fir stands of California. Jour. Forestry 49: 192-196, illus.

51. ______, and ______
1956. Seed crops of forest trees in the pine region of California. U. S. Dept. Agr. Tech. Bul. 1150, 48 pp.

52. Gail, F. W., and J. W. Long
1935. A study of site, root development and transpiration in relation to the distribution of Pinus contorta. Ecology 16: 88-100.

53. Gill, L. S.
1954. Dwarfmistletoe of ponderosa pine in the Southwest. Rocky Mountain Forest & Range Expt. Sta., Sta. Paper 14, 9 pp. /Processed./

54. Haasis, F. W.
1921. Relations between soil type and root form of western yellow pine seedlings. Ecology 2: 292-303, illus.

55. ______
1923. Frost heaving of western yellow pine seedlings. Ecology 4: 378-390, illus.

56. Harlow, William M., and Elwood S. Harrar
1937. Textbook of dendrology (Covering the important forest trees of the United States and Canada). McGraw-Hill Book Co., Inc. 527 pp., illus.

57. Helmers, A. E.
1943. Ecological anatomy of ponderosa pine needles. Amer. Midland Nat. 29: 55-71.

58. Herman, F. R.
1954. A guide for marking fire-damaged ponderosa pine in the Southwest. Rocky Mountain Forest & Range Expt. Sta. Res. Note 13, 4 pp. /Processed./

59. Holtby, B. E.
1947. Soil texture as a site indicator in the ponderosa pine stands of southeastern Washington. Jour. Forestry 45: 824-825.

60. Howell, Joseph, Jr.
1931. Clay pans in western yellow pine type. Jour. Forestry 29: 962-963.

61. ______
1932. The development of seedlings in ponderosa pine in relation to soil types. Jour. Forestry 30: 944-947.

62. Iloff, P. M., Jr., and N. T. Mirov
1954. Composition of gum turpentines of pines XIX. A report of Pinus ponderosa from Arizona, Colorado, South Dakota, and northern Idaho. Amer. Pharm. Assoc. Jour. Sci. Ed. XLIII (6): 373-378.

63. Keen, F. P.
1938. Insect enemies of western forests. U. S. Dept. Agr. Misc. Pub. 273, 280 pp. Revised 1952.

64. ______
1940. Longevity of ponderosa pine. Jour. Forestry 38: 597-598.

65. ______
1943. Ponderosa pine tree classes redefined. Jour. Forestry 41: 249-253.

66. Korstian, C. F.
1924. A silvical comparison of the Pacific Coast and Rocky Mountain forms of western yellow pine. Amer. Jour. Bot. 11: 318-324, illus.

67. ______, and W. H. Long
1922. The western yellow pine mistletoe: Effect on growth and suggestions for control. U. S. Dept. Agr. Bul. 1112, 36 pp., illus.

68. Krauch, Herman
1922. The intolerance of western yellow pine regarded as a regulating factor in the maintenance of the type. Jour. Forestry 20: 463-464.

69. ______
1924. Acceleration of growth in western yellow pine stands. Jour. Forestry 22: 639-642.

70. ______
1949. Growth after cutting in an even-aged mature ponderosa pine stand. Jour. Forestry 47: 296-299, illus.

71. Lachmund, H. G.
1923. Relative susceptibility of incense-cedar and yellow pine to bole injury in forest fires. Jour. Forestry 21: 815-817.

72. Lane, R. D., and A. L. McComb
1948. Wilting and soil moisture depletion by tree seedlings and grass. Jour. Forestry 46: 344-349, illus.

73. Leaphart, Charles D.
1955. Preliminary observation on a current outbreak of western gall rust (Cronartium coleosporioides). Plant Disease Reporter 39(4): 314-315, illus.

74. Lightle, Paul C.
1954. The pathology of Elytroderma deformans on ponderosa pine. Phytopathology 44: 557-569.

75. ______
1955. Experiments on control of Elytroderma needle blight of pines by sprays. Calif. Forest & Range Expt. Sta. Forest Res. Note 92, 6 pp. /Processed./

76. Little, Elbert L., Jr.
1953. Check list of native and naturalized trees of the United States (including Alaska). U. S. Dept. Agr., Agr. Handbook 41, 472 pp.

77. Lloyd, F. E.
1898. On hypertrophied scale-leaves in Pinus ponderosa. N. Y. Acad. Sci. Ann. 11: 45-54.

78. Long, W. H.
1924. The self-pruning of western yellow pine. Phytopathology 14: 336-337.

79. Lynch, Donald W.
1951. Diameter growth of ponderosa pine in relation to the Spokane pine-blight problem. Northwest Sci. 25: 157, 163.

80. ______
1953. Growth of ponderosa pine on best sites. North. Rocky Mountain Forest & Range Expt. Sta. Res. Note 128, 4 pp., illus. /Processed./

81. ______
1954. Growth of young ponderosa pine stands in the Inland Empire. Intermountain Forest & Range Expt. Sta., Res. Paper 36, 16 pp. /Processed./

82. Maguire, William P.
1955. Radiation, surface temperature, and seedling survival. Forest Sci. 1: 277-285.

83. ______
1956. Are ponderosa pine crops predictable? Jour. Forestry 54: 778-779.

84. Meinecke, E. P.
1928. The evaluation of loss from killing diseases in the young forest. Jour. Forestry 26: 283-298.

85. Merriam, C. Hart
1898. Life zones and crop zones of the United States. U. S. Biological Survey Bul. 10, 79 pp.

86. Meyer, Bernard S., and Donald B. Anderson
1946. Plant physiology. D. Van Nostrand Co., Inc. New York 696 pp., illus.

87. Meyer, Walter H.
1931. Effect of release upon the form and volume of western yellow pine. Jour. Forestry 29: 1127-1133, illus.

88. ______
1938. Yield of even-aged stands of ponderosa pine. U. S. Dept. Agr. Tech. Bul. 630, 60 pp., illus.

89. Mielke, James L.
1952. The rust fungus *Cronartium filamentosum* in Rocky Mountain ponderosa pine. Jour. Forestry 50: 365-373.

90. Mirov, N. T.
1938. Phylogenetic relations of Pinus jeffreyi and Pinus ponderosa. Madroño 4: 169-171.

91. ______ 1940. Tested methods of grafting pines. Jour. Forestry 38: 768-777.

92. ______ 1941. Distribution of growth hormone in shoots of two species of pines. Jour. Forestry 39: 457-464.

93. ______ 1944. Experiments in rooting pines in California. Jour. Forestry 42: 199-204.

94. ______ 1954. Chemical composition of gum turpentine of pines of the United States and Canada. Jour. Forest Products Res. Soc. 4: 1-7.

95. ______ 1954. Studies of the chemical composition of turpentine of the genus Pinus in relation to taxonomy. 8th Internatl. Bot. Cong. (Paris), 8 Sec. 2,4(6): 47-49.

96. ______ 1954. Apache pine and its relationship to ponderosa pine. Madroño 12(8): 251-252.

97. ______, J. W. Duffield, and A. R. Liddicoet
1952. Altitudinal races of Pinus ponderosa--12-year progress report. Jour. Forestry 50: 825-831.

98. Mowat, Edwin L.
1950. Cutting lodgepole pine overstory releases ponderosa pine reproduction. Jour. Forestry 48: 679-680.

99. Munger, Thornton T.
1917. Western yellow pine in Oregon. U. S. Dept. Agr. Bul. 418, 48 pp., illus.

100. ______ 1947. Growth of ten regional races of ponderosa pine in six plantations. Pacific Northwest Forest & Range Expt. Sta. Forest Res. Note 39, 4 pp. /Processed./

101. Munns, E. N.
1922. Reproduction and nitrogen. Jour. Forestry 20: 497-498.

102. Munns, E. N.
1922. Bear clover and forest reproduction. Jour. Forestry 20: 745-754.

103. ______
1938. The distribution of important forest trees of the United States. U. S. Dept. Agr. Misc. Pub. 287: 1-176.

104. Neils, George, Lowell Adams, and Robert M. Blair
1956. Management of white-tailed deer and ponderosa pine. Jour. Forestry 54: 238-242.

105. Olson, D. S.
1932. Seed release from western white pine and ponderosa pine cones. Jour. Forestry 30: 748-749.

106. Orr, Leslie W.
1954. The 1953 pine butterfly outbreak in southern Idaho and plans for its control in 1954. Intermountain Forest & Range Expt. Sta. Misc. Pub. 1, 12 pp., illus. /Processed./

107. Parker, Johnson
1953. Annual trends and cold hardiness of ponderosa pine and grand fir. Ecology 34: 377-380.

108. Paul, Benson H.
1955. Resin distribution in second-growth ponderosa pine. U. S. Dept. Agr. Forest Products Lab. Report 2046, 6 pp.

109. Pearson, G. A.
1924. Studies in transpiration of coniferous tree seedlings. Ecology 5: 340-347.

110. ______
1931. Forest types of the southwest as determined by climate and soil. U. S. Dept. Agr. Tech. Bul. 247, 144 pp., illus.

111. ______
1950. Management of ponderosa pine in the Southwest. U. S. Dept. Agr., Agr. Monog. 6. 218 pp., illus.

112. ______
1951. A comparison of the climate in four ponderosa pine regions. Jour. Forestry 49: 256-258.

113. Pike, Galen W.
1927. The relation of the viability of seed to the age of the parent tree. Univ. of Idaho Forest Club Annual 9: 7-18.

114. Pike, G. W.
1934. Girdling of ponderosa pine by squirrels. Jour. Forestry 32: 98-99.

115. Righter, F. I.
1945. Pinus: the relationship of seed size and seedling size to inherent vigor. Jour. Forestry 43: 131-137.

116. ______, and J. W. Duffield
1951. Interspecies hybrids in pines. Jour. Hered. 42: 75-80.

117. ______, and ______
1951. Hybrids between ponderosa and Apache pine. Jour. Forestry 49: 345-349.

118. Roe, Arthur L., and A. E. Squillace
1950. Can we induce prompt regeneration in selectively cut ponderosa pine stands? North. Rocky Mountain Forest & Range Expt. Sta. Res. Note 81, 7 pp. /Processed./

119. Roeser, Jacob, Jr.
1932. Transpiration capacity of coniferous seedlings and the problem of heat injury. Jour. Forestry 30: 381-395.

120. ______
1941. Some aspects of flower and cone production in ponderosa pine. Jour. Forestry 39: 534-536.

121. Salman, K. A., and J. W. Bongberg
1942. Logging high-risk trees to control insects in the pine stands of northeastern California. Jour. Forestry 40: 533-539.

122. Schorger, A. W.
1913. An examination of oleoresins of some western pines. U. S. Dept. Agr. Forest Serv. Bul. 119, 36 pp.

123. Schubert, G. H.
1952. Germination of various coniferous seeds after cold storage. Calif. Forest & Range Expt. Sta. Forest Res. Note 83, 7 pp. /Processed./

124. ______
1953. Ponderosa pine cone cutting by squirrels. Jour. Forestry 51: 202.

125. ______
1954. Viability of various coniferous seeds after cold storage. Jour. Forestry 52: 446-447.

126. Schubert, G. H.
1955. Effect of storage temperature on viability of sugar, Jeffrey, and ponderosa pine seed. Calif. Forest & Range Expt. Sta. Forest Res. Note 100, 3 pp. /Processed./

127. ______
1956. Effect of ripeness on the viability of sugar, Jeffrey, and ponderosa pine seed. Soc. Amer. Foresters Proc. pp. 67-69.

128. Shaw, Charles Gardner, George W. Fischer, Donald F. Adams, Mark F. Adams, and Donald W. Lynch
1951. Flourine injury to ponderosa pine: a summary. Northwest Sci. 25(4): 156.

129. Siggins, Howard W.
1933. Distribution and rate of fall of conifer seeds. Jour. Agr. Res. 47: 119-128.

130. Society of American Foresters
1954. Forest cover types of North America (exclusive of Mexico). 67 pp.

131. Sparhawk, W. N.
1918. Effect of grazing upon western yellow pine reproduction in central Idaho. U. S. Dept. Agr. Bul. 738, 31 pp., illus.

132. Squillace, A. E.
1953. Effect of squirrels on the supply of ponderosa pine seed. North. Rocky Mountain Forest & Range Expt. Sta. Res. Note 131, 4 pp. /Processed./

133. ______, and Lowell Adams
1950. Dispersal and survival of the seed in a partially cut ponderosa pine stand. North. Rocky Mountain Forest & Range Expt. Sta. Res. Note 79, 4 pp. /Processed./

134. Starker, T. J.
1934. Fire resistance in the forest. Jour. Forestry 32: 462-467.

135. Stone, Edward C., and Harry A. Fowells
1955. Survival value of dew under laboratory condition with *Pinus ponderosa.* Forest Sci. 1(3): 183-188.

136. Sudworth, George B.
1908. Forest trees of the Pacific slope. U. S. Dept. Agr. Forest Serv. 441 pp., illus.

137. Sudworth, George B.
1917. The pine trees of the Rocky Mountain region. U. S. Dept. Agr. Bul. 460, 47 pp., illus.

138. Tarrant, Robert F.
1953. Soil moisture and the distribution of lodgepole and ponderosa pine. Pacific Northwest Forest & Range Expt. Sta. Res. Paper 8, 10 pp. /Processed./

139. Taylor, W. P., and D. M. Gorsuch
1932. A test of some rodent and bird influences on western yellow pine reproduction at Fort Valley, Flagstaff, Arizona. Jour. Mammal. 13: 218-223.

140. Thornthwaite, Charles Warren
1931. Climates of North America. Geog. Rev. 21: 633-644.

141. U. S. Forest Service
1935. Annual report. Intermountain Forest & Range Expt. Sta. /Processed./

142. ______
1936. Annual investigative report. Intermountain Forest & Range Expt. Sta. /Processed./

143. ______
1937. Annual investigative report. Intermountain Forest & Range Expt. Sta. /Processed./

144. ______
1940. Annual report. Intermountain Forest & Range Expt. Sta. /Processed./

145. ______
1948. Woody-plant seed manual. U. S. Dept. Agr. Misc. Pub. 654, 416 pp., illus.

146. ______
1955. Timber Resource Review, Chapter IX, Appendices. A summary of basic statistics. (Preliminary draft subject to revision.)

147. U. S. Weather Bureau
1954. Climatological data. California Annual Summary 1954. LVIII(13).

148. Wagener, Willis W., and Marion S. Cave
1946. Pine killing by the root fungus (*Fomes annosus*) in California. Jour. Forestry 44: 47-54, illus.

149. Weaver, Harold
1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific slope. Jour. Forestry 41: 7-14, illus.

150. Weaver, John E., and Frederic E. Clements
1938. Plant ecology. Second edition. McGraw-Hill Book Co., Inc. New York and London. 601 pp., illus.

151. Weidman, Robert H.
1921. Forest succession as a basis of the silviculture of western yellow pine. Jour. Forestry 19: 877-885.

152. _______, R H.
1939. Evidences of racial influences in a 25-year test of ponderosa pine. Jour. Agr. Res. 59: 855-888.

153. _______
1947. Trees in the Eddy Arboretum. Calif. Forest & Range Expt. Sta. Forest Res. Note 53, 8 pp. /Processed./

154. Weir, James R.
1916. Hypoderma deformans, an undescribed needle fungus of western yellow pine. Jour. Agr. Res. 6: 277-288, illus.

155. Whiteside, John M.
1951. The western pine beetle. U. S. Dept. Agr. Cir. 864, 10 pp., illus.

156. Wilson, Alvin K.
1952. Rodent damage in ponderosa pine plantations. Intermountain Forest & Range Expt. Sta. Res. Note 3, 2 pp. /Processed./

157. Woolsey, Theodore S., Jr.
1911. Western yellow pine in Arizona and New Mexico. U. S. Dept. Agr. Forest Serv. Bul. 101, 64 pp., illus.

MISC. PUB. NO. 12 JUNE 1957

by

JAMES D. CURTIS & DONALD W. LYNCH

INTERMOUNTAIN FOREST & RANGE EXPERIMENT STATION
FOREST SERVICE
U. S. DEPARTMENT OF AGRICULTURE
OGDEN, UTAH
REED W. BAILEY, DIRECTOR